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STUDIES OF GASTROPODA.

II. FULGUR AND SYCOTYPUS.

AMADEUS W. GRABAU.

THE following brief account of the shell-development in Fulgur and Sycotypus, and its bearing on our knowledge of the succession of species in time is a summary of studies carried on for some years in various museums, especially the National Museum at Washington, the museums of the Academy of Natural Sciences and of the Wagner Free Institute, at Philadelphia the American Museum of Natural History, the Museum of Comparative Zoölogy at Cambridge, and the museum of the Boston Society of Natural History. To the officers of all these Institutions I am greatly indebted for many privileges and helpful suggestions.[1]

The fulguroids are a particularly interesting group on account of their extra-limital distribution. Disregarding a few questionable reports of the alleged finding of these shells in other regions, we find their geographical range in modern as well as Tertiary times to be along the Atlantic coast of North America, from the south shore of Cape Cod, to the Gulf of Mexico. The peculiarly restricted distribution of this group is explained by the fact, that the animal on leaving the egg capsule is without a velum. This latter, though well developed and large before hatching, (see Figs. 1 and 2) is dropped just before the animal emerges from the capsule, and after the shell is already well developed. Thus the meroplanktonic stage, which we may assume existed in the ancestors of Fulgur and Sycotypus, was apparently suppressed even in the earliest species of Fulgur, as otherwise the distribution would be more world-wide. Actual migration is prevented by the differences in temperature of the water and by the ocean currents. This condition of affairs has existed in this region in all probability since Miocene times.

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[1] I wish especially to mention the names of Dr. W. H. Dall, Prof. H. A. Pillsbry, Mr. C. W. Johnson, Prof. R. P. Whitfield, Dr. L. P. Gratacap, Dr. W. Mc. M. Woodworth, Prof. R. T. Jackson, and above all, the late Professor Alpheus Hyatt, as those who have most materially assisted me in my studies of the Gastropoda.

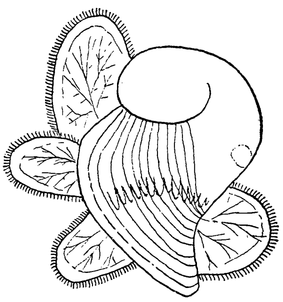

FIG. 1. *Sycotypus canaliculatus* just before emerging from the egg capsule; showing the shell, gills, heart, and large velum. × 13.5.

SHELL DEVELOPMENT IN FULGUR AND SYCOTYPUS.

The earliest shell stage, *i. e.* the protoconch, may be studied easily in *Fulgur caricum* and *Sycotypus canaliculatus*. It is generally preserved in the adult shell, and may also be readily obtained from the egg capsules, particularly in the autumn, when embryos in all stages of development are found often in the same string of capsules. This protoconch consists of a single smooth volution, with no apparent markings; not even lines of growth are visible. If however a young

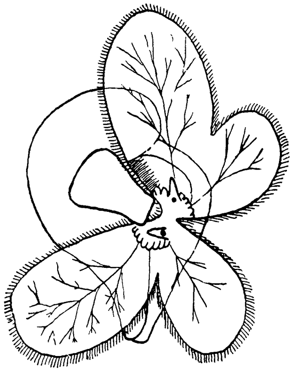

FIG. 2. *Sycotypus canaliculatus.* Ventral view of specimen Fig. 1, showing foot, tentacles, eyes, and velum jus before it is lost. × 13.5.

individual is taken from the egg capsule before the shell has assumed its distinctive characteristics, very faint lines of growth may be seen, as well as indistinct radiating lines. These features have been particularly observed in young *Sycotypus canaliculatus*, as noted in a previous paper.[1] In this early stage the shell is also umbilicated, and since there is no anterior canaliculation as yet, this stage has the characteristics of a Natica shell. I have elsewhere referred to this as the naticoid stage of the protoconch, and noted its very general occurrence in gastropods.[2] This naticoid stage recalls the characters of early gastropods, such as *Straparollina remota* of the Lower Cambric, which I have tentatively considered as close to the protogastropod.

The protoconch of *Fulgur caricum* generally merges into the early conch stage (the nepionic[3]), without any visible line of demarkation between the two. Occasionally, however, such a division does exist, in the form of a strong growth line. In *Sycotypus canaliculatus* this line of demarkation appears more frequently, while in *Buccinum undatum* it is, so far as noted, a constant character. In this latter type, the change is often emphasized by an angulation in the whorl.

The nepionic stage of shell growth begins with the second whorl. The outermost portion of the lip becomes gradually extended into the incipient anterior canal so characteristic of the adults of these shells. In Fulgur and Sycotypus this notch or incipient anterior canal, occurs at some distance outward from the umbilical margin of the lip, and hence as growth progresses the protoconch will have its plane of coiling tilted at an angle to that of the plane of coiling of the succeeding whorls. This gives the protoconch the characteristic oblique appearance found in many canaliculate (siphonate) types. This pattern is less pronounced in Buccinum and Fasciolaria. In consequence of this change of plane of coiling the second whorl partly buries the earliest portion of the first whorl or protoconch.

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[1] Studies of Gastropoda. *Amer. Nat.* vol. 36, p. 925, fig. 8.

[2] *Loc. cit.* p. 919.

[3] The Hyattian terminology of stages in development [ontogenetic] is: *nepionic* or babyhood; *neanic* or youthful; *ephebic* or adult, and *gerontic* or senile. Each stage is furthermore divisible into 3 substages indicated by the use of the prefixes *ana*, *meta*, or *para*. The prefix *phyl-* or *phylo-* refers to the corresponding stage of racial development, *i. e.*, the phylum; thus: *phyloneanic*, *phylephebic*, *phylogerontic*, etc.

For about half a volution or less, the shell is smooth, although lines of growth become more pronounced. At more or less regular intervals stronger lines of growth appear (ananepionic). In the later portion of the nepionic stage (metanepionic) longitudinal wrinkles or ribs appear which characterize the ambital portion of the whorl, and may be traced upward to the suture between the two whorls. At about the same time or, in some cases, apparently earlier, faint revolving lines become visible on the shell. They are nearly uniform, those on the ambitus being slightly stronger. They represent the earliest part of the primary spirals so pronounced in later stages. Almost immediately after the inception of the vertical wrinkles or ribs, an angulation appears a little above the ambitus of the whorl, which thus becomes divided into shoulder and body portion. At the same time the ribs become stronger on the angulation, where they soon assume the character of tubercles in a single row from the obsolescence of the ribs above and below the angulation. As the shoulder above the angulation broadens, two new spiral lines appear on it between the suture and the shoulder angle. These, with progressive growth, are augmented by the appearance of new ones alternately on each side of the first two. At this stage the operculum is already well developed (Figs. 3 and 4)

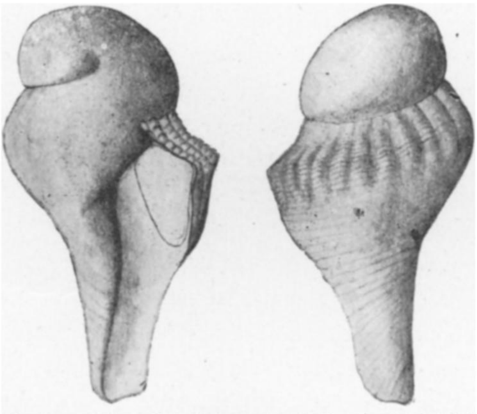

FIG. 3. *Fulgur carica.* The young shell taken from the egg capsule. × 11.5.

In *Sycotypus canaliculatus* the large velum (Figs. 1 & 2) is lost at about the time of formation of tubercles on the shoulder angle, and this may be considered the end of the metanepionic period, shortly after which the animal passes from the egg capsule. I have not examined *Fulgur caricum* at this stage, but there can be little doubt that the conditions are essentially similar. The shell-characteristics of these two types and of Buccinum and Fasciolaria at hatching are indicated in figure 18. The last or paranepionic period, distinguished by a tuberculated angulation (Fig. 4), is brought to a close in *S. canaliculatus* by the formation of the characteristic sutural canal. This, in some individuals, appears to have just begun on the lip at the period of hatching, but usually it begins only toward the end of the second volution. At this stage, the early neanic, the lines of growth are well marked and of nearly equal strength with the revolving lines, the two together giving the shell surface a reticulated appearance. The sutural canal is bounded by a strong revolving ridge, between which and the row of nodes on the angle, lies the sunken and flat or slightly concave shoulder. On this shoulder three distinct spirals are defined, at the beginning of the neanic stage, *i. e.*, the third conch volution. Shortly before the beginning of the fourth volution of the conch (the fifth counting the protoconch) a fourth spiral appears on the shoulder, close to the ridge bounding the sutural canal. A little later a fifth appears just within the line of nodes. Shortly after this, the neanic stage comes to an end, the shoulder ridge losing its nodes and continuing as a simple keel. This occurs between the fourth and fifth volutions of the conch. At the same time the inner ridge becomes less prominent, and the shoulder consequently level instead of sunken. At about this time (end of fourth volution) a sixth spiral appears on the shoulder, next to the inner ridge, and half a volution later

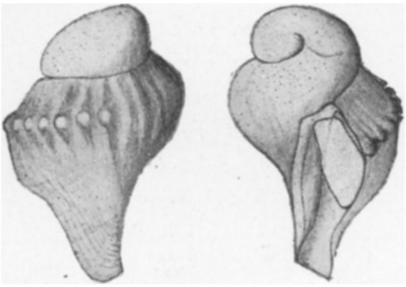

FIG. 4. *Sycotypus canaliculatus*, the young shell taken from the egg capsule. × 11.5.

a seventh, next to the keel. Finally an eighth spiral appears on the sutural side before the completion of the fifth conch volution. All these spirals soon become of nearly uniform size, while a second cycle of spirals begins to appear between those of the first cycle as they diverge with the increase in width of the shoulder. A supplementary spiral also appears just within the sutural canal, next to the bounding ridge. Where these spirals are crossed by the lines of growth, short, pointed, horny spines are found on the periostracum. On the body of the shell intercalation begins much earlier than on the shoulder. In accelerated individuals intercalated spirals appear earlier on the shoulder.

Sycotypus pyrus of the modern Floridian fauna seems to be a more accelerated type. The smooth and ribbed stages are passed through quickly, occupying only about half a volution. The tubercles continue to the end of the second conch volution, after which a smooth keel succeeds. When the shell has reached the size where, in *S. canaliculatus*, the tubercles change into the smooth keel (between the fourth and fifth volutions), the keel in *S. pyrus* begins to disappear, and the curvature of the outer lip becomes uniform. In large (adult) individuals the carina has generally disappeared altogether, and the lip is rounded uniformly. This produces the "excavatus" type of lip. The canal begins in the second volution of the conch. In two old Floridian shells of *S. pyrus*, in the collection of the American Museum of Natural History, the canal becomes narrower and less pronounced in the last whorl, and in some instances it disappears altogether for a short space. In a characteristic specimen five spirals have developed by the end of the first conch volution. The sixth appears immediately after the beginning of the second volution, and the seventh begins in the third volution. Near the end of this volution intercalated spirals (of the second series) also appear, while in *S. canaliculatus* these generally do not appear until the beginning of the sixth volution. In this species the amount of embracing varies, thus changing the elevation of the spire.

ANCESTRAL SPECIES.

An immediate ancestor of *S. pyrus* seems to be *S. pyriformis* (Conrad) from the late Miocene of the Natural Well, Duplin Co., North Carolina.[1] In this species the tubercles continue nearly as long as those of *S. canaliculatus*; they become obsolete on about the fifth volution and are succeeded by a keel. The last portion of the sixth volution is rounded, as in adult *S. pyrus*. *S. pyriformis* is therefore a less accelerated type than *S. pyrus*, and fulfills all the requirements of the immediate ancestor of the latter.

The next earlier representative of the series seems to be a form from the Miocene of Faison, N. C., and probably referable to *S. canaliferus* (Conrad) Gill. The type of this species is from the early Pliocene (Waccamaw beds of South Carolina, Tuomey and Holmes), and is a more advanced type, not far removed from the recent *S. canaliculatus*. (See *Busicon canaliculatum*, Tuomey and Holmes, *Pliocene Fossil Shells of N. Carolina*, pl. 29, fig. 2). This species is considered by Dall as the ancestor of *S. canaliculatus*. It fulfills the requirements of such a relationship, in that the keel is tuberculated throughout. While *S. canaliculatus* has advanced only one stage beyond *S. canaliferus* *S. pyrus* and *S. pyriformis* have passed two stages beyond this. Therefore a species of the *S. pyrus* type only as far advanced as *S. canaliculatus*, *i. e.*, one in which the last whorl is keeled but not rounded, might be looked for in the upper Miocene. These conditions seem to be satisfied by species occurring in the late Miocene beds of Faison Mt. Pass, North Carolina.

Other specimens found in these later Miocene beds of Faison, N. C., show well the manner of formation of the sutural channel in retarded as well as primitive types. In the simplest specimen seen, a flattening appears near the suture in the third whorl of the conch. This becomes wider, more pronounced, and faintly depressed, and the shoulder has four simple revolving spirals. This condition continues to the end of the specimen (a young one with five volutions), while the shoulder angle at the same time retains its tubercles. In more advanced specimens the flattening, which begins earlier, is bordered by a carina arising in the third or fourth whorl of the conch, while the shoulder becomes excavated below this. The tubercles of the shoulder angle cease about a whorl later and a simple carina succeeds. In a still more accelerated specimen the flattening next to the suture is depressed on the formation of the bounding carina on the third whorl, while acceleration is also shown by the presence of intercalated spirals on the shoulder of that whorl. In the accelerated types the depressed sutural canal becomes triangular from the development of the bounding carina into a strong posterior notch. This is emphasized, as acceleration increases, by the disappearance of the shoulder angle; which gives us, when the spire is low, the type named by Conrad *Busicon excavatus* (Fig. 5) but a type very different in appearance when high. (See *S. elongatus* Gill, *Am. Jour. Conchology*, Vol. 3, p. 150). Finally in these beds (Magnolia, Duplin Co., Smithsonian collection, 114540) occur specimens showing every gradation between *S. excavatus* and the extremely accelerated type described by Tuomey and Holmes as *Cassidulus carolinensis* (Fig. 6) from the Pliocene (?) of South Carolina. The "excavatus" type of aperture is, however, not confined to one line of descent, but crops out in parallel lines, *i. e.*, is a homoplastic character. This is shown by old age, or accelerated individuals of modern *Sycotypus pyrus* and by specimens referred to *S. pyrus* from the Pliocene of Shell Creek, Fla. (Natl. Mus.). These shells can therefore not be classed together as one species. Apparently *S. excavatus* led to *S. carolinensis*, and with that this branch became extinct in the Miocene. The slight development of the sutural channel in some of these specimens is probably to be explained as a case of retardation in development,

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[1] *Am. Journ. Conch.* Vol. 3, 1867. p. 265, pl. 20, fig. 1.

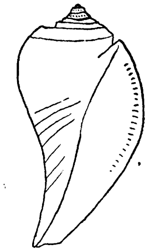
FIG. 5. *Sycotypus excavatus.* × ½. After Conrad.

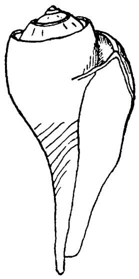
FIG. 6. *Sycotypus carolinensis.* After Tuomey and Holmes. × ½.

recalling the characters of the late Oligocene ancestors of the series. (See beyond.)

Another branch, which became extinct in the Miocene, is that of *S. incilis* (Conrad). This is primitive or retarded as far as the shoulder spirals are concerned, for they never reach the second cycle, but become obsolete after the third or fourth primary spiral has appeared. The change in this series is toward a progressive widening of the sutural canal, until, in some adults, it is wider at the lip than the shoulder. The ridge bounding it becomes very pronounced, so as to form a prominent posterior notch. This notch separates more and more from the body of the shell as the sutural canal becomes wider, until finally it occupies nearly the position which is occupied by the shoulder angle in *S. canaliculatus* (Fig. 7a). The shoulder angle becomes almost or

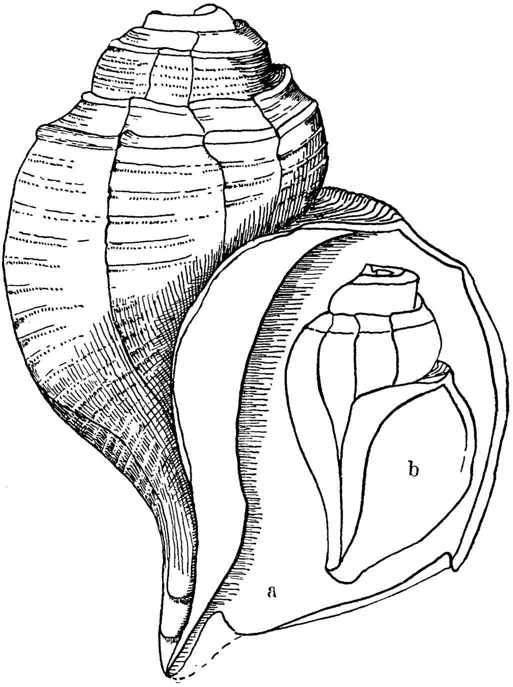

FIG. 7. *Sycotypus incilis.* An extreme old-age type (a) and an elongate phylogorontic variety (b). From specimens in the palæontologic collections of Columbia University. × ½.

quite obsolete in the more accelerated individuals, thus giving the lip a rounded "excavatum" form. Here the notch made by the sutural ridge is the strongest element, having entirely replaced the original notch of the outer or keel portion. This is commonly accompanied by a looser coiling, because the succeeding whorls clasp below the middle of the preceding one instead of above it, as in *S. canaliculatus*. *S. incilis* developed in the mid-Miocene Yorktown beds, and terminated in a high-spired and short-canaled form with prominent sutural channel and obsolete shoulder angle. (Fig. 7b.) A form of this kind is not unlike in appearance to that of an old Buccinum in which the last whorl has been partially separated. The spirals of the shoulder are always few in number, and generally simple; indicating an offshoot from a primitive line with few spirals, or a partial retardation affecting this feature. This small number of spirals, in *S. incilis* seems to be due to the rapid widening of the sutural channel and the consequent encroachment of the bounding ridge on the shoulder space. The latter remains always narrow, thus preventing a material increase in the number of spirals.

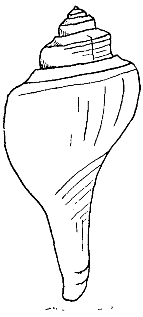

FIG. 8. *Sycotypus alveatus.* × ½. After Conrad.

Apparently in the direct line of ancestry of *S. incilis* is *S. alveatus* (Conrad) (Fig. 8). This preserves the keel throughout and has the strong ridge bordering the sutural channel. With our present knowledge we may perhaps regard *S. alveatus* as the radicle of this line, which seems to have branched off from the main line in Miocene time. The changes are towards a high spire and a profound sutural canal, terminated by an excavatum-like lip. *S. incilis* may therefore be considered as representing a phylogerontic branch in mid-Miocene time which was not propagated beyond that period.

In the Duplin beds occurs a high-spired form described by Tuomey and Holmes as *S. conradii*, but referred by Conrad to *S. incile*. This I believe to be a distinct branch, which seems to be a derivative from the excavatus line and a parallel to *S. incilis*. In *S. conradii* the spirals remain comparatively few and the whorls embrace below the middle. The sutural canal remains narrow, however, and the shell has more nearly the aspect of *S. canaliculatus*. Intermediate types connect this with *S. excavatus* and *S. canaliferus*.

The ancestral type of these branches of Sycotypus is probably close to *S. rugosus* (Conrad) in most characters (Fig. 9). This Mid-Miocene species retains its tubercles throughout, though these become very prominent in certain varieties and almost spine like in the later whorls. The channel already begins in the late third or early fourth whorl, hence this is no new character. The number of spirals is simple throughout, as far as observed, but there are seven of them fully formed in the fourth or fifth whorl. In some specimens the shoulder tubercles begin to unite into a strong ridge.

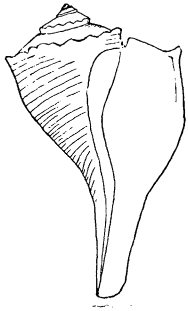
Fig. 9. *Sycotypus rugosus.* × ½. After Conrad.

In *S. coronatus* we have a form which compares in the character of the sutural canal with the ancestral type, but which has the tubercles strongly developed and the spirals intercalated at an early stage, showing acceleration in these points. Another terminal type, *S. concinnus*, Conr. has simpler spirals and a coronatus-like shoulder angle, which is however more compressed and projects more than in that species.

The ancestral type of these species of Sycotypus is probably to be sought in the Upper Oligocene mutations named by Dall. *tampaensis* and *perizonatus*, and referred as varieties to Conrad's *Fusus spiniger*. In the former of these, seven simple spirals occur on the shoulder and a smooth space between the suture and the first spiral in front of it. In the latter, intercalation of secondary spirals begins on the shoulder after the fifth simple one has appeared, and the smooth space next to the suture becomes depressed into a canaliculation. The mutation *burnsii* Dall of the Upper Oligocene, seems to be still more primitive in generally having only nodules with coarse and few spirals, and the suture scarcely channeled. It appears that the specimens classed together under the name of *Fulgur spiniger* Conrad are not of monophyletic origin. An examination of Conrad's type from Vicksburg, Miss., in the collection of the Academy of Natural Sciences at Philadelphia shows it to have a protoconch of the Levifusus type. This consists of about two and one-half volutions; the apical whorl is minute, and the succeeding ones enlarge gradually. An angulation is formed by two spirals, above which the shoulder becomes gently concave. The upper spiral becomes stronger and alone forms the echinations in the later whorls. Riblets appear early after the shell has become angulated and these are soon reduced to mere tubercles. After two whorls the latter become strong enough to be called spines.

In the Lower Miocene of the Chipola River, Florida, occurs a type with true Fulgur protoconch, which has been referred to *F. spiniger*. This, together with the species referred by Dall to *F. nodulatum*, appear to be lateral branches from the main stem which led to the modern types. Conrad's *S. nodulatus* has the aspect of another extreme type of the Levifusus series, though it may turn out to be a true Fulgur.

At this time, as Dall has well said, the sutural canal was not a well fixed character, having but just made its appearance. It was hardly of specific and certainly not of generic value, but soon after, in the Middle Miocene, it became well established and fixed in the Sycotypus line of development, which henceforth became an independent branch, with only occasional reversions to a faint sutural canal.

On searching for the Eocene ancestor of the fulgurs we apparently find it in a type from the Lower Clairborne of Texas, which has been identified with *Levifusus pagoda* Heilprin. This type, however, differs from Heilprin's species in having a true Fulgur protoconch, whereas *L. pagoda* has a three-whorled naticoid protoconch with gradually enlarging volutions ornamented in the latter portion by semilunar riblets. This type of protoconch is characteristic of many species of Pleurotoma, to which Levifusus seems to be closely related. But in the Texan type the obliquely elevated, swollen fulguroid protoconch is smooth for a little over a whorl and then is furnished with fine vertical ribs which merge into those of the round-whorled succeeding portion of the shell. There are at least two round whorls with simple ribs and simple spirals, after which the shoulder flattens out and the ribs become faint toward the suture. An angulation appears on the whorl, formed at first by two strong spirals, but later, the upper becomes strongest and causes the formation of rather flattened blunt serrations. Intercalated spirals appear on the sixth whorl.

This shell, though much smaller than the Fulgurs, has all the characteristics required for an immediate ancestor. It must, of course, be separated from *Levifusus pagoda,* Heilprin, and I propose to designate it *Levifusus ? harrisi*, after Professor Gilbert D. Harris, whose indefatigable labors in the Tertiaries of the Gulf region have brought together a wealth of material which may serve as a basis for further phylogenetic study. Both Dall and Harris consider Levifusus in the line of ancestry of Fulgur; the latter, indeed, regards *L. pagoda* Heilprin as the prototype of the Fulgurs. The protoconch of the ordinary form of *L. pagoda* does not satisfy the conditions of such an ancestor, but that of the Texan form does. Whether or not these two types are to be considered congeneric remains to be determined; further investigation may show that the changes from a normal naticoid type of protoconch to the oblique swollen Fulgur type occurred in this genus. We may well believe that at first the form remained unstable, oscillating between the two types, but by the time Fulgur had developed, that feature no doubt, had become stable. At the same time fulguroid types were probably developed from the normal *Levifusus pagoda*, the result being such types as "*Fulgur*" *spiniger* Conrad, which, as already noted, is not a true Fulgur. Spiniger-like forms were also developed among the true Fulgurs, the similarity of forms in both cases being explainable as an instance of parallelism. "*Fusus*" *quercollis* Harris from the Midway stage, and "*Fusus*" *rugatus* Aldrich from the Lignitic, seem to be related to the ancestors of Fulgur. These types, for which the generic name Fulgurofusus is proposed have a fulguroid protoconch, while the early whorls are almost identical with those of Fulgur. The adult *F. quercollis* has the Fulgur characters of whorl grafted upon a Fusus form. This type is more accelerated in that its whorls become angular as early as do those of Fulgur, and it is not impossible that this type may be in direct line of ancestry of Fulgur. In that case *Levifusus ? harrisi* cannot be considered as in the direct line of ancestry.

THE SPECIES OF FULGUR.

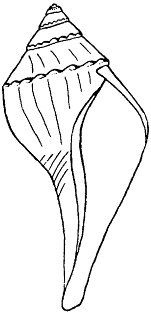

FIG. 10. *Fulgur fusiformis*, × ½. After Conrad.

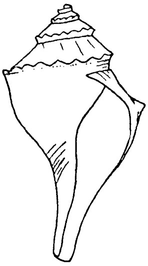

FIG. 11. *Fulgur tuberculatum*. Outline of Conrad's figure (Med. Tert. pl. 46, fig. 2) × ½.

In turning now to typical species of Fulgur, we find *F. fusiformis* (Fig. 10) to be the most primitive Mid-Miocene type. In this the simple nodules remain to the end ; they are replaced by a smooth rounded keel only in accelerated or old age individuals. This species is not far removed from the Lower Miocene or Oligocene ancestor, which gave rise to the two lines of descent, *i. e.* Sycotypus and Fulgur. From *Fulgur fusiformis* on the one hand is derived the large and ponderous *Fulgur maximum* Conr. of the Yorktown beds (Fig. 13), in which the tubercles are found only in the young stage, while the adult is smooth and round-whorled. Probably a phylogerontic derivative of this is the variety *tudiculatum* from the upper bed at Alumn Bluff. In this the final whorl reaches up so as to rise slightly above the preceding ones. *Fulgur carinatum* Conr. (Fig. 12) on the other hand, is derived from *F. fusiformis* probably through *F. tuberculatum* (Fig. 11) by a consolidation of the tubercles into a continuous keel, which characterizes the last and one or more of the preceding whorls. In some

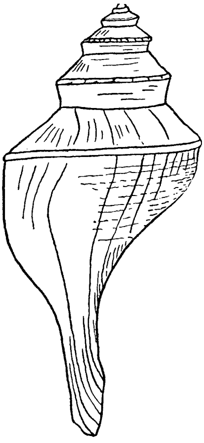

FIG. 12. *Fulgur carinatum*. × ½. After Conrad.

specimens of *F. tuberculatum*, from St. Mary's river, Md., the nodes are replaced in the last whorl by a continuous strong and smooth keel, while in others the nodes still persist faintly on the keel of the last whorl. The more strongly spinous types of *F. tuberculatum* represent lateral radiations. In general the angular character of the whorl is retained for a brief period before the whorl becomes rounded to the maximum stage, but no true keel has been observed between the tuberculous and the smooth stages. In Fusus, on the contrary, a definite keel is generally formed by the consolidation of the tubercles, as in *Sycotypus canaliculatus* and *Fulgur carinatum*. In Fusus, a round-whorled condition follows the keel, but no spines of the *Fulgur caricum* type are known in any true Fusus. Similarly, a round-whorled condition follows the keel in advanced species of Sycotypus (*S. pyrus*, etc.). Such a condition we may expect in *S. canaliculatus* in old age types or in future accelerated descendants of the present types. Examples of *Fulgur carinatum* may yet be found with the final whorl rounded.

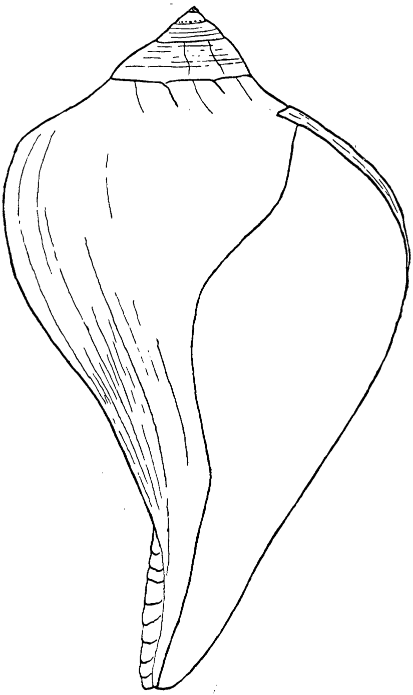

FIG. 13. *Fulgur maximum*. × ½. After Conrad.

It appears then, that there are two branches of development in the Fulgur series, one leading to a keeled condition and probably never forming spines, the other to a smooth and then spinous condition. The latter branch was the successful one among the fulgurs, while the former condition succeeded in Sycotypus. The keeled branch occurred in the Miocene fulgurs but did not persist. Some of the early Sycotypus developed echinations by an accentuation of the tubercles, but these did not prove successful.

Hemifusus and Melongena represent the spinous line among the Fusidæ, which seems to have been equally successful with the non-spinous line of Fusus proper. In such types as *Hemifusus colosseus*, a strong line or spiral persists for a time after the tubercles have become obsolete. This I have formerly spoken of as a keel, but it represents merely the natural transition from tuberculous to round stage. A similar faintly carinate shoulder angle occurs again in most cases, before the spines appear.

In company with *Fulgur maximum* is a variety (var. A of Conrad) in which spines are found on the last whorl. These spines are a new feature and are not to be confounded with the tubercles of the earlier whorls. The latter are the remains of the ribs on the shoulder angle, while the spines are periodic emarginations of the lip on the line of the shoulder angle. In the early successors of *F. maximum* these spines occur only on the final whorl, but in progressively accelerated types they come in earlier and earlier, having the appearance of being pushed back on the whorls. *Fulgur tritonis* Conrad (Fig. 14) is a type from the Mid-Miocene of Yorktown, Va., in which spines appear after a short period of a round-whorled condition. The spines gradually increase in size until they are equal to those of the modern *F. caricum*. Two branches are met with here: *F. tritonis* Conrad with a normal anterior canal, leading to *F. caricum*; and *F. filosum* Conrad with a strong oblique fold on the anterior canal in the later whorls, leading to *F. eliceans* Montf. of the modern Fauna.

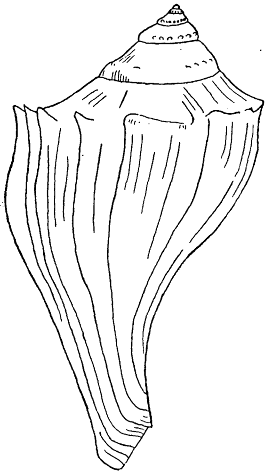

FIG. 14. *Fulgur tritonis*. × ½. After Conrad.

The modern *F. caricum* and *F. eliceans* are produced from their respective ancestors *F. tritonis* and *F. filosum* by an acceleration of the spinous stages, which are crowded back until the *maximum* stage is dropped out altogether and the spines follow immediately upon the tubercles, and even encroach upon them, thus causing a perfect gradation from tubercles to spines. *F. caricum* makes its appearance in the Waccama beds of the Carolinas while *F. eliceans* has, so far as I know, been reported only from the modern Fauna. From *F. eliceans* we finally derive the variety *candelabrum* Lam., in which there are only three or four huge spines in the last whorl.

In the late Miocene (Duplin beds of S. Carolina) and the early Pliocene (Caloosahatchee beds of Florida) a parallel series seems to have developed independently from an ancestor of the *F. fusiformis* type. In these formations occur round-whorled and spiralled shells of the *maximum* type (Fig. 13) except that they are much more strongly contracted in front of the body whorl than the Yorktown species. This gives the anterior portion of the shell a slender fusiform aspect unlike that of *Fulgur caricum*.[1] Heilprin (*Trans. Wag. Free Inst. of Sci.*, vol. 1, p. 73) describes typical *Fulgur maximum* from the Caloosahatchee beds of Florida. I have not seen these shells, which, if Heilprin's diagnosis is correct, represent the last survivors of that Mid-Miocene type. The Pliocene type is a variety of *F. rapum* Heilpr. without spines. (Fig. 15.) It is

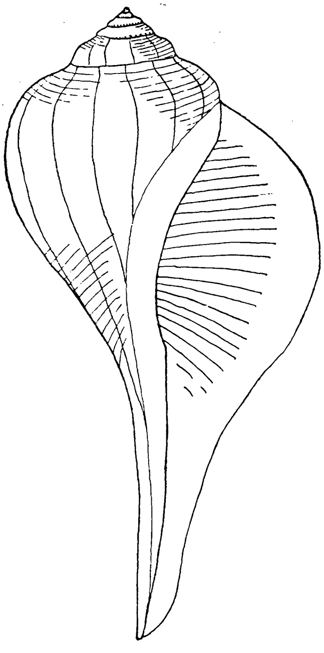

Fig. 15. *Fulgur rapum*. Smooth variety. From a specimen in the Willcox collection. American Mus. Nat. Hist. × ½.

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[1] Dall states that in all the members of the genus "the females have a wide patulous canal, while the canal in male specimens is much narrower and more cylindrical." (Loc. cit. p. 115.) The difference between the specimens from the Late Miocene and Early Pliocene, and typical *F. maximum* from the Mid-Miocene, is greater than can be accounted for by sexual differences alone.

the immediate ancestor of typical *F. rapum*, and appears to connect it with *F. maximum* or *F. fusiformis*. *F. rapum* differs merely in having faint suggestions of spines on the shoulder, which has again assumed an angular outline; but this is not continuous. It represents the first stage in the development of the *caricum* features. The spines of this species are small and may be compared to the first formed portion of a spine in adult *F. caricum*, or to abortive spines in the same species. This form is probably the morphic equivalent of Conrad's *F. maximum* var. A, from the Mid-Miocene beds. More accelerated specimens with a similarly contracted form have the spines fully developed in the last whorl, and hence parallel *F. tritonis*, from which they differ only in the more slender form. This may be called *F. rapum* var. *tritonoides*. The terminal member of this branch appears to be the Floridian *Fulgur coarctum* Sowerby, which has been considered a dextral *F. perversum*, but which I believe to be of independent origin, since its ancestors are found in the Pliocene strata of the adjoining region. The interior of the shells of this series is strongly lirate, and the shells are generally thin.

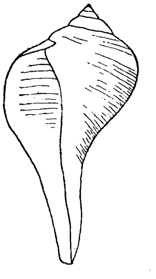

FIG. 16. *Fulgur contrarium*. × ½. After Conrad.

Turning now to the reversed fulgurs, we find in *F. contrarium* (Fig. 16) of the Late Miocene and Early Pliocene (Duplin and Caloosahatchee beds) a form comparable to the smooth variety of *F. rapum* of the same horizons. This form is knobbed in the early whorls, and rounded and smooth (except for the spirals) in the later ones. It is similar to *F. rapum* in having the same slender contracted end. It seems, from our present knowledge of the shell characters and of the geologic succession of the mutations, that the separation of the slender series into dextral and sinistral forms occurred in the Late Miocene, and that the two branches have remained separate ever since. Leidy and Willcox[1] have figured a series of reversed Fulgurs showing the gradual transition in characters from the smooth type *F. contrarium* to the modern spinous type, *F. perversum*. The series is exactly parallel to that leading from *F. maximum* to *F. caricum* and from *F. rapum* to *F. coarctum*, although the species correspond in form to the second rather than the first branch, as already noted. The sinistral type corresponding to *F. rapum* Heilpr. may be designated *F. obrapum* nom. nov.;[1] while that corresponding to *F. tritonoides* is Conrad's *Fulgur adversarium* (Am. Journ. Conch. vol. III, p. 185). This species is figured by Tuomey and Holmes[2] as *Fulgur perversum*, and by Leidy and Willcox[3] as *F. contrarium* and *F. perversum* respectively. The final member of this series is *F. perversum* (Leidy and Willcox, figs. 6 and 7) from the Pliocene and modern faunas of the Gulf region. This corresponds to *F. coarctum* of the same fauna, which, as already stated, is considered by Tryon and others a dextral *F. perversum*. In Fig. 17 is represented the early nepionic stage of *Fulgur perversum*.

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[1] *Proc. Wag.* Free *Inst.*, vol. 3, pl. 9 and 10.

In the Miocene marls of Cape Fear river, N. C., associated with *Fulgur filosum*, occurs a reversed type with the same characters. For purposes of designation I will apply to this the name of *Fulgur obfilosum*, nom. nov. This may represent merely a reversed condition of *F. filosum*, or it may be a member of a distinct series, developed independently and parallel to the dextral series. In its earlier stages, it is a *Fulgur adversarium* developing the characteristic fold only in the adult. This suggests that it may have been derived from that type, though the present unsatisfactory knowledge of the vertical distributions of these fossils makes it impossible to state whether or not they are in proper chronologic relation. A reversed type with the characters of *F.*

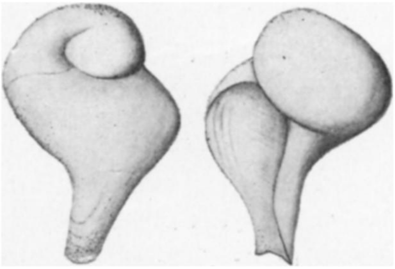

Fig. 17. *Fulgur perversum*. Young shell taken from the egg-capsule. × 10.

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[1] Leidy and Willcox, pl. 9 and 10, fig. 3; fig. 2 represents a *perversum* type in which a faint angularity occurs on the shoulder of the final whorl.

[2] *Pliocene Fossil Shells of N. Carolina*, pl. 29, fig. 3.

[3] *loc. cit.*, pl. 9, 10, figs. 4 and 5.

eliceans, described by Phillippi as *F. kieneri* Phil., occurs in the modern fauna of the south coast.[1] This may be merely a reversed *F. eliceans*, but it seems more likely that it was independently derived from the reversed Miocene type just mentioned (*F. obfilosum*).

The table at the end of the article indicates the probable genetic relationships of the species under discussion.

VARIATIONS IN THE SPINES OF ADULT FULGUR CARICUM.

Normally the spines of *F. caricum* are uniform in the adult, but individual variation is quite marked here. The final whorls of this species are generally marked by a series of color bands, or strong growth lines, which indicate a resting stage following a growth period. Each growth period begins with a non-spinous shoulder condition, and the spine begins to form only in the last half or last third of the period. At the end of the period the spine is at its maximum, and opens forward. With the beginning of the next growth period, the spine is closed anteriorly, or more rarely, is abandoned abruptly and floored over at the base, remaining open in front. Not infrequently the period is shortened, when the spine is only partially or not at all developed. This may perhaps be a pathologic condition. Sometimes the spine makes its appearance only toward the end of its normal period, and hence is small. This character, due to retardation, repeats the ancestral state of the spines in types like *F. maximum* var. A Conr. (compare *F. rapum*), where it was normal. Again, a period may be lengthened, when the spine will be larger than the normal. Such is the normal condition in *F. candelabrum*, where each period constitutes a third or a fourth of a volution.

In general, when the periods are of normal length, we find a gradual decrease in the number of periods in a volution as the shell increases in size. Thus in a number of individuals with normal periods, the average for the fifth, sixth, and seventh volutions (including the protoconch) were 14, 13, and 12 respectively. Out of thirteen specimens, the average for the 6th and 7th volutions were 12 and 11 periods respectively, while 13 for the 5th volution is not uncommon. In old age or pathologic individuals the number of periods in the last portion of the final whorl becomes much greater as the periodic additions to the shell between resting stages are much shorter. Thus it appears that in normal progressive types the period increases in length as the shell increases in size, and at a rate more rapid than the increase of the shell. The number of spines on each succeeding whorl is therefore fewer. Judged by this standard, *F. eliceans* must be considered more accelerated than *F. caricum*. In *F. eliceans* the average periods for the 5th, 6th, and 7th volutions are more nearly 12, 9, and 6 respectively. Finally, in *F. candelabrum* we have extreme acceleration in this respect, as the final whorl is provided with only three periods and spines.

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[1] Kiener, pl. 9, fig. 2; Tryon, vol. 3, pl. 57, fig. 390; *F. gibbosum* Conrad. *Proc. Acad. Nat. Sci. Phila.*, 1862, p. 286.

Relatives of Fulgur and Sycotypus.

Among the near relatives of Fulgur and Sycotypus in the modern fauna we may mention Fasciolaria and Buccinum. A comparison of the early (ananepionic) shell stage of these two forms with Fulgur and Sycotypus in the same stage of development shows a very close similarity. (Compare Fig. 18.) Leav-

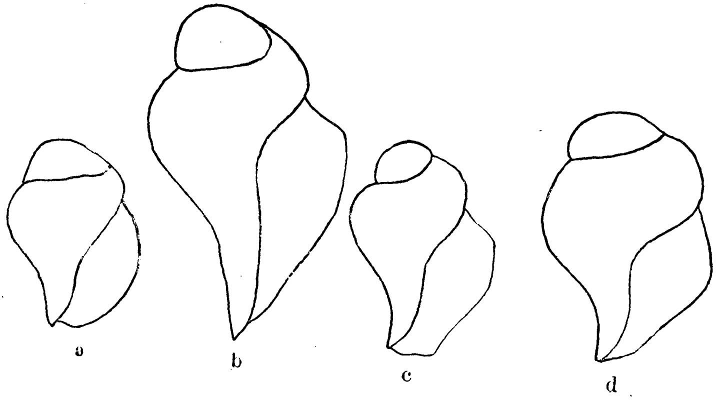

Fig. 18. Outline cf young Fasciolarioid shells. a. *Buccinum undatum*, b. *Fulgur caricum*, c. *Sycotypus canaliculatus*. d. *Fasciolaria gigantea*. × 10.

ing aside differences in size, we find that Fulgur has the longest anterior canal, Buccinum the shortest, while that of Fulgur is the narrowest, that of Sycotypus is the widest and most patulous. Fasciolaria is the most ventricose of the series. In spite of these differences, there is an unmistakable family resemblance between the four young individuals, a resemblance, which in the case of Fulgur and Sycotypus is retained even in the adults. In *Buccinum undatum* spirals appear in the metanepionic stage, and ribs at a later period. In *Fasciolaria gigantea* ribs appear first (Fig. 19), the spirals afterwards. This therefore seems to be nearer to Fulgur in which the same order of succession of features obtains. It is therefore evident, that we must look to the Mesozoic fasciolarioid shells for the ancestors of these types.

The development of plications on the columella has been shown by Dall to be due to a relative retreat of the muscle of fixation from the aperture, and the consequent crowding and folding of the mantle. This feature appears in a large number of phyletic series, and must be regarded as a secondary acquisition. In the fasciolarioid ancestors of the present types, such plications could not have existed, since they do not occur in Fulgur and Sycotypus, nor in the young Fasciolaria. We know too little about the Cretacic forms at present to determine what species are in the line of ancestry of the types under consideration. Pyropsis or Pyrifusus, both of which are well repre-

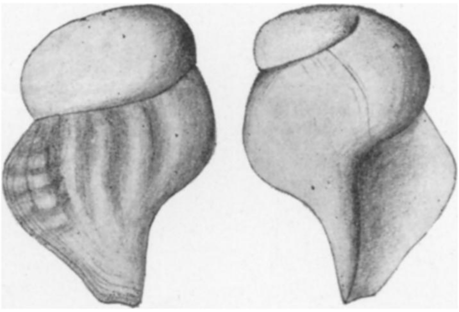

FIG. 19. *Fasciolaria gigantea ?* Young shell taken from the egg capsule. × 10.

sented in the Atlantic coast Cretacic, may represent the Miocene progenitor, both having so far as I have been able to ascertain, the characters requisite for such ancestry. These may lead on the one hand to the Eocene levifusoid ancestor of the Fulgurs, and on the other hand to Fasciolaria through such forms as Odontofusus, with but a single columellar plication.[1]

Fusus, Hemifusus and Melongena are not directly related to Fulgur. Fusus at least existed before Fulgur, having already acquired its highly accelerated protoconch in the Eocene. Fusus seems to be an Old World type, which did not reach the American coast until Post-Eocene time, so far as indicated by evidence now available.[2] Hemifusus is an accelerated descendant of Fusus, with fulguroid form,[3] while Melongena is a phylogerontic terminal member of that series. Thus it appears that the Fusidæ and the Fasciolaridæ (the latter with branches leading to Fulgur on the one hand and to Buccinum on the other) have been distinct since pre-Eocene time, and that their common ancestor must be looked for in the Cretacic if not earlier.

I am well aware that to class Buccinum and Fulgur with Fasciolaria, and Melongena and Hemifusus with Fusus, subordinates lingual dentition to shell characters. The odontophores of Fusus and Fasciolaria are similar, and different from those of the other genera mentioned. In these again the type of dentition is similar, though minor significant differences occur. It seems to me that where the shell characters point the other way, mere similarity of dentition is insufficient to establish relationship, but must be explained rather as parallelism.

We know nothing of the lingual dentition of the Tertiary and earlier species, and but little of that of modern types. Furthermore we know nothing of the changes, if any, which the dentition undergoes in the development of the animal and so cannot use lingual ontogeny as index of genetic relationship. The dental apparatus of Buccinum and Fulgur is very similar, and that of Hemifusus and Melongena is nearly identical. In both groups, the outer members or marginals of the adult odontophore bear each one large and one or more small denticles, while the median is supplied with small denticles only. In Fasciolaria and in Fusus so far as known, the marginals are furnished with numerous nearly equal denticles. If we assume that in the ancestral type both marginals and median had one or at the most only a few denticles, it is easy to see how the multidenticulate type of modern Fasciolaria may be developed along one line, and the similar type of modern Fusus along a parallel line. It is also easy to see, that the heterodenticulate types of modern Buccinum and Fulgur could branch off from the primitive fasciolarioid ancestor, by the accentuation of the outer denticle of each marginal. Again the simple melongenoid type could branch off from the primitive fusoid type, and develop by a similar accentuation of the outer denticle. I see therefore no sufficient reason in the similarity of odontophores for the present classification of these genera, and instead of uniting Fulgur and Hemifusus-Melongena in one family, and Fusus and Fasciolaria in another, I feel that the development of the shell characters show very clearly the close relationship of Fusus and Hemifusus-Melongena, and of Fasciolaria and Fulgur, with Buccinum not far removed.

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[1] See Whitfield: *Gastropoda and Cephalopoda of the Raritan Clays and Greensand Marls of New Jersey.* Monograph 18 U. S. Geol. Survey.

[2] The American Eocene species of Fusus so far described do not belong to that genus. See Grabau: *American Naturalist*, vol. 36, p. 922.

[3] For illustration of protoconch and early conch of Hemifusus see Grabau *loc. cit.* p. 921, fig. 5.

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TABLE OF THE GENETIC RELATIONSHIPS OF THE SPECIES OF FULGUR AND SYCOTYPUS.